THE INCREASE IN EXTENSOR TONUS IN TOTALLY OR PARTIALLY CEREBELLECTOMIZED CATS DURING WEIGHTLESSNESS

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There are reports in the literature [3-6, 9-12, 16] indicating that the disturbances of coordination of movements and of orientation in space arising in the condition of weightlessness are mainly due to changes in the functions of the vestibular apparatus.

Direct investigations of the functions of the labyrinths of waking cats during transient (1-2 sec in duration) weightlessness arising during free falling [9] have shown that both the frequency and the amplitude of the biopotentials of the vestibular ganglion were almost doubled. The study of the electrical activity of the cerebral cortex of the cat [5] has shown that the most obvious and characteristic changes during weightlessness of short duration took place in the anterior portion of the suprasylvian and ectosylvian gyri, regarded as the location of the cortical representation of the vestibular function.

In the conditions of weightlessness changes take place in the level of bioelectrical activity of the cerebellum [18]. Information has been obtained indicating changes in the frequency of the electrical discharges of the brainstem neurons of Deiters' nucleus during polarization of the anterior lobes of the cerebellum and of the labyrinths [8, 15], and there is evidence showing convergence of labyrinthine, optic, and proprioceptive stimuli on the cerebellum [1, 11, 14], suggesting the participation of the cerebellum in motor coordination and spatial orientation.

To examine the role of the cerebellum in the formation of postural and motor reactions in weightlessness, experiments were carried out on cerebellectomized animals.

EXPERIMENTAL METHOD

Experiments were carried out on four cats. The cerebellum of one animal was removed 4 months before the experiments. At the time of the experiments the main sign of the "dynamic period" accompanying cerebellectomy —extensor rigidity of the limbs—was completely absent; the animal could walk only for a very short distance, and then only along the wall, while compensation of the act of standing appeared one month after this operation. The ansiform lobes [1, 11] with the adjacent dorsal and ventral paraflocculus were removed from another cat 5 months before the experiments. The volume of cerebellar tissue removed from these cats is shown in Fig. 1. The technique of removal of the cerebellum and the character of some of the motor disorders are described elsewhere [2]. The two intact cats were used as controls.

The state of weightlessness was produced in an airplane flying along a parabolic trajectory. The duration of each period of weightlessness was 28-30 sec. The weightlessness was preceded and followed by overloading not exceeding 1.8-2.0 g for a period of up to 15 sec. In individual experiments the state of weightlessness was produced without the preceding overloading. The animals were placed in a special container on board the airplane. The behavioral reactions of the animals were recorded on motion pictures. Each animal was subjected to the action of weightlessness 12 times. In some experiments, to exclude movements of expectancy in relation to the nearest surface, the animals' eyes were covered with a mask.

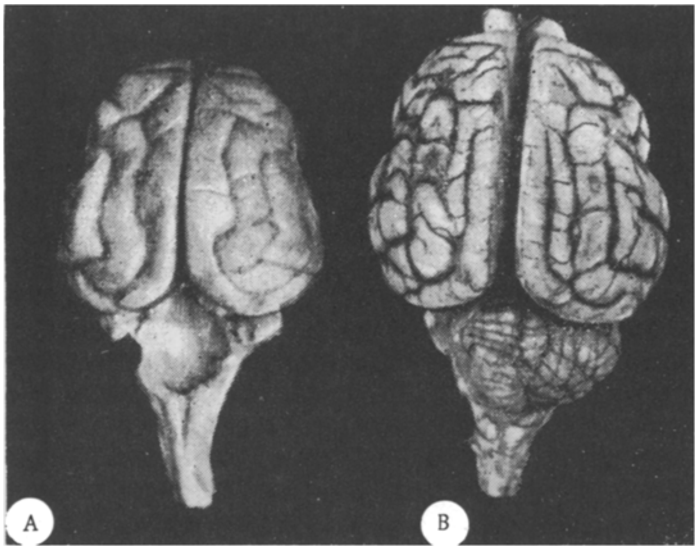

Fig. 1. Preparations of the animals' brain. A) with totally removed cerebellum; B) with partially removed cerebellum.

Before the experiments in weightlessness began and after they had ended, the vestibular function of the animals was tested both in the presence and absence of vision. Investigations were made of the head- and limb-lifting reflexes, the reflex of readiness to jump, the righting reaction, and the orienting reflexes.

EXPERIMENTAL RESULTS

In the conditions of weightlessness in mammals a sharp increase takes place in the motor activity (movements with elements of "running," grasping movements, scratching, stabilizing movement of the tail), which in the initial stage of adaptation to weightlessness occur against the background of a characteristic predominance of the extensor tonus of the spinal, neck, and limb muscles [3, 4]. Similar signs of discoordination in weightlessness were also observed in the present experiments in the intact animals. However, this was found only during the first exposures to weightlessness, and later when the action of weightlessness was repeated the animals gradually adapted themselves to the changed gravitational conditions and their motor activity diminished appreciably. For instance, haphazard sweeping movements of the paws ceased in the 3rd period of weightlessness, a posture with extended spine and limbs was no longer observed in the 4th-5th period, and turning of the tail ceased after the 7th period. Exclusion of vision in the intact cats (by means of a mask) slightly increased the motor activity of the animal until the 7th period of weightlessness, but starting from the 8th-9th period the absence of vision had no effect on movement of the animals. The five successive and most characteristic poses of a normal cat in one of the later periods of weightlessness are illustrated in Fig. 2, I, a-e.

In contrast to the normal cats, the characteristic feature of the cerebellectomized cat was a well-marked state of extensor rigidity of the muscles of the trunk, the neck, and the posterior and especially the anterior extremities (Fig. 2, II), greatly exceeding the analogous changes in the tonus of the control animals even in the first periods of weightlessness: the animal waved its rigid limbs about, flexing them only at the shoulder and hip joints, and rotated its almost straight tail (Fig. 2, II, c-e). In the course of 12 experiments no diminution of these phenomena was observed on account of adaptation to weightlessness. Rhythmic, swinging movements of the limbs (1-2 per sec) were observed only during the first 4-6 periods of weightlessness, in the course of which the animals unsuccessfully tried to grasp surrounding objects but could not hold them because of the considerable predominance of the extensor tonus in the limbs.

In the cerebellectomized animal, the exclusion of vision had practically no effect on the character of its motor activity in the conditions of weightlessness. In the partially cerebellectomized cat a well-marked increase in motor activity was observed and the animal tried to grasp suropunding objects, during which an asymmetrical contraction of the trunk muscles occurred, stronger on the side opposite the operation, so that the longitudinal body axis was bent to the right and the animal turned to the left (Fig. 2, III, c-e): at first the head turned, then the fore part of the

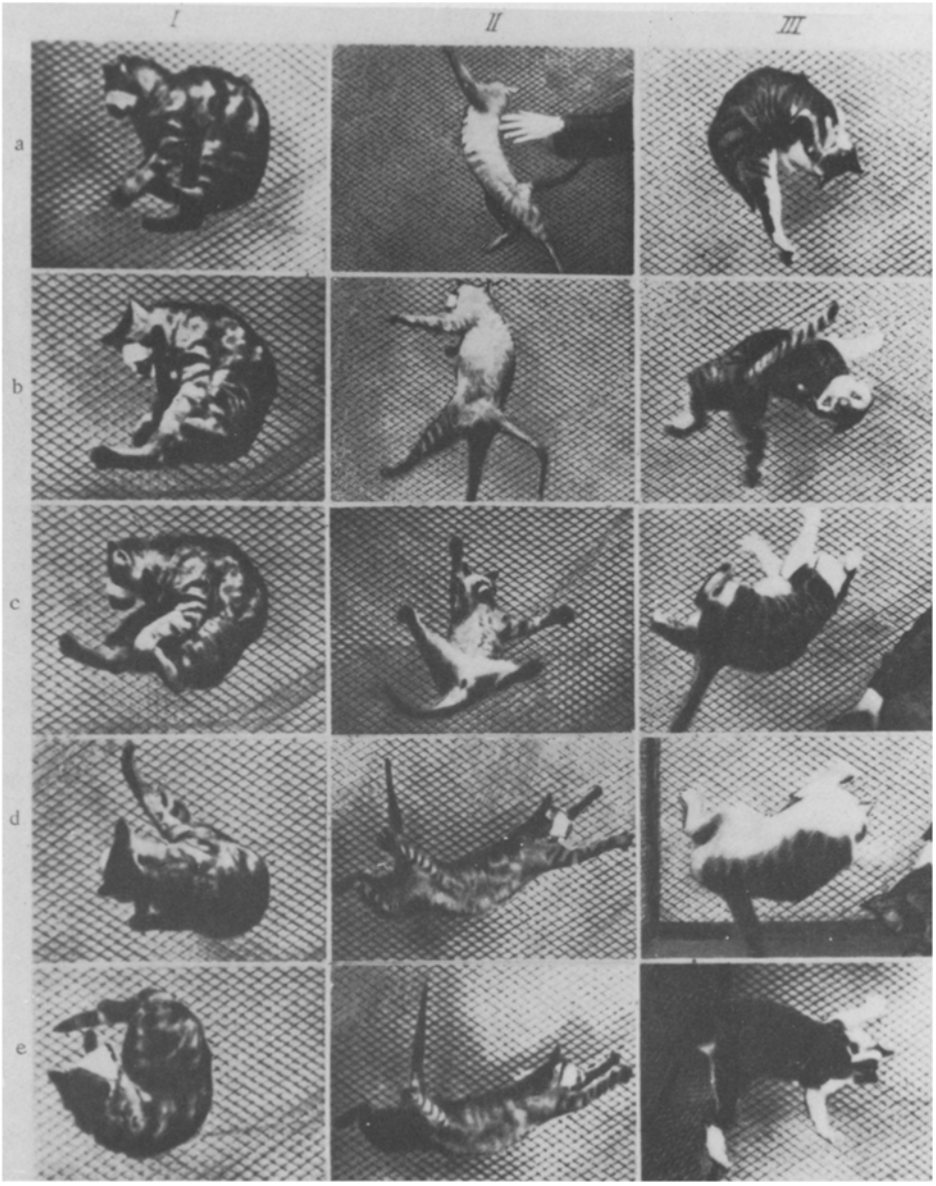

Fig. 2. Animals in weightlessness. I) intact animal during 10th period of weightlessness; II) cerebellectomized animal during 11th period of weightlessness; III) animal from which the left cerebellar hemisphere had been removed, during 12th period of weightlessness. a-e—frames of films.

trunk, and lastly the hind part. The continuous turning movements of the tail were seen to take place towards the side opposite to that of rotation of the trunk. If the animal succeeded in grasping surrounding objects, the movements described quickly ceased. In the case of exclusion of vision, the motor excitation of the animal was appreciably intensified.

Comparison of the results of tests of the vestibular function of the experimental animals before and after the experiments in weightlessness revealed no differences. The brisk vestibular reflexes of the intact animals indicated the normal functioning of the vestibular analyzer (Fig. 3, I, a-e).

The postural vestibular reflexes of the cerebellectomized animal also were preserved, although their character was modified by dyskineses: the orienting reflexes of the trunk and head and the lifting reflexes of the limbs took place against the background of increased extension of the limbs and trunk (in contrast to the intact animal); the

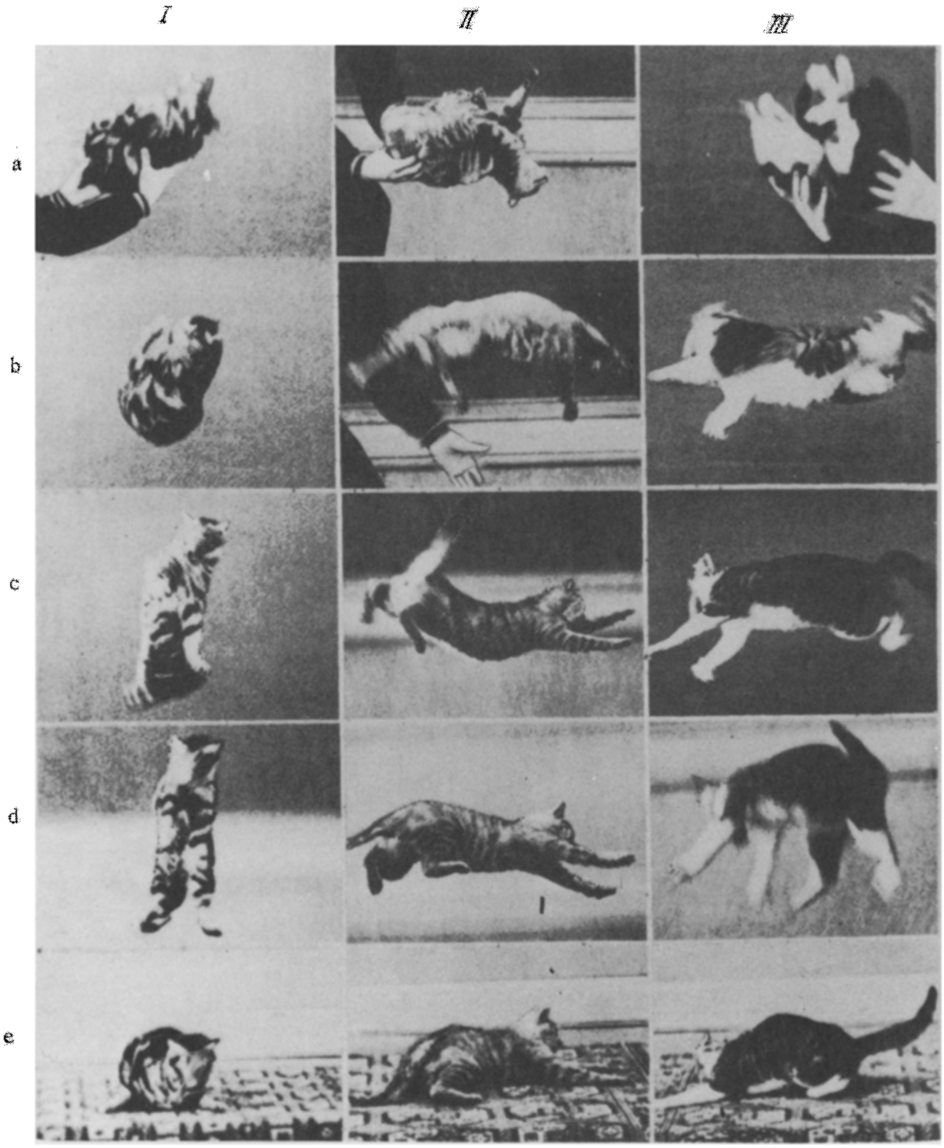

Fig. 3. Righting reaction. I) intact animal. a) released from the hands; b) 0.25 sec later; c) 0.5 sec later (a complete turn); d) 0.75 sec later; e) landing; II) cerebellectomized animal; III) hemicerebellectomized animal: a) released from the hands; b) 0.125 sec later; c) 0.25 sec later (a complete turn); d) 0.75 sec later; e) landing.

reflex of readiness to jump was well marked, while the righting reaction took place actually faster than in the intact animal. Whereas in the control animal one complete turn took 0.5 sec (Fig. 3, I, c), the same action was accomplished by the cerebellectomized animal in 0.25 sec (Fig. 2, II, b). Unlike the intact animal, the cerebellectomized cat failed to make a soft landing, and after landing it stepped backward.

In the partially cerebellectomized animal all the vestibular reflexes were appreciably increased: the righting reflex took place more quickly than in the intact and totally cerebellectomized animals; a complete turning of the trunk for landing was accomplished 0.2 sec after releasing the animal from the hands in the position with its limbs uppermost (Fig. 2, III, c). The turning movement was made with the left shoulder, and during falling asymmetry of the trunk (flexed to the right) and marked extension of the forelimb on the side of the operation were observed (Fig. 2, III-V; c-e). Vestibular tests carried out on the partially cerebellectomized animal produced a marked rise in its aggressiveness.

Our experiments showed that in totally or partially cerebellectomized cats extensor rigidity arose in a state of weightlessness. Similar phenomena were also observed in normal animals, although they were less marked in degree and they disappeared as adaptation to weightlessness developed.

On the ground, hypertonus of the extensors appears in the early periods after cerebellectomy in animals ("cerebellar release" [7]) or after decerebration ("decerebrate rigidity"). In the first case it is explained by removal of the tonic inhibitory action of the fastigial nuclei of the cerebellum on the vestibular nuclei of the brain stem [8, 17]. The cerebellar nature of the extensor facilitation is also demonstrated by the experimental application of strychnine to the cortex of the paleocerebellum [18]. In the second case the hypertonus is associated with removal of the cortical and mesencephalic inhibitory influences. An important role in the regulation of postural tonus is played by impulses from the labyrinths [6, 14] and from the receptors of the skin and muscles [7].

According to electromyographic findings [6], in decerebrate animals the tonus of the extensors is lowered during weightlessness, while in cerebellectomized animals, as the present investigation has shown, on the contrary it is raised.

Compensation of the "sign of release" of the cerebellum takes place mainly on account of the inhibitory influence of the brain stem and spinal cord [7], and also to some extent of the cortex [14]. However, this compensation cannot fully replace the cerebellar inhibition, so that the adaptation to weightlessness which is observed in normal cats could not be found in the cerebellectomized cats in our experiments.

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